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## Energetic limitation of avian parental effort: Field experiments in the kestrel (*Falco tinnunculus*)

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**Key words:** Avian energetics; brood size; reproductive strategies.

### Abstract

We studied the limiting factors for brood size in the kestrel, *Falco tinnunculus*, by measuring parental effort in natural broods of different size and parental response to manipulation of food satiation of the brood. Parental effort was quantified as total daily time spent in flight, and total daily energy expenditure, from all-day observations.

During nestling care males with different natural brood sizes (4 to 7 chicks), spent an average of  $4.75 \text{ h} \cdot \text{d}^{-1}$  in flight independent of brood size, and expended an average total daily energy of  $382 \text{ kJ} \cdot \text{d}^{-1}$ . Due to a higher flight-hunting yield (mammal-prey caught per hour hunting), males with larger natural broods were able to provision their broods with the same amount of food (mainly *Microtus arvalis*) per chick ( $62.6 \text{ g} \cdot \text{d}^{-1}$ ), with the same effort as males with smaller broods. This provisioning rate was close to the mean feeding rate of hand-raised chicks in the laboratory, that were fed *ad libitum*, ( $66.8 \text{ g} \cdot \text{d}^{-1} \cdot \text{chick}^{-1}$ ).

Our food deprivation experiments revealed that male kestrels strongly respond to food shortage in the nest. In the older nestling phase males on average increased their daily rate of food delivery to the nest as a response to experimental food deprivation by almost three times to  $646.4 \text{ g} \cdot \text{d}^{-1}$ , by increasing their flight activity level from 4.46 to  $8.41 \text{ h} \cdot \text{d}^{-1}$ . This increased energy expenditure was sustained, for as long as eleven days, by increasing the metabolizable energy intake up to what is presumed to be the maximum rate. Even under considerable experimental food stress (chicks not being satiated due to continuous removal of

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delivered food by the observers) about half of the available daylight time remained unused for foraging.

We conclude 1) that the mean daily energy expenditure of males during nestling care – to which clutch size is apparently initially adjusted – is well below the maximum they are able to sustain and 2) that the energy expenditure they can sustain under extremely high nestling demand is not set by the available time for foraging or the available energy in the environment. Thus the birds normally operate well below their presumed maximum, and only during food shortage, e.g., as caused by our experiments, do they increase activity up to this maximum. Therefore we conclude that the kestrels have costs other than energy expenditure, such as parental survival, that are involved in the increased “cost” of parental effort.

We discuss possible generalisations about existing energetic limitations during parental care in altricial birds. From published estimates of daily energy expenditure during parental care ( $DEE_{par}$ ) in 30 different bird species we derived the equation:  $DEE_{par} = 14.26 \text{ kg}^{0.65} \text{ Watt}$ . This relationship differs significantly in slope ( $T = -2.49$ ;  $p < 0.02$ ) from the allometric equation for the maximum rate of energy assimilation ( $DME_{max}$ ) as provided by Kirkwood (1983):  $DME_{max} = 19.82 \text{ kg}^{0.72} \text{ Watt}$ . In smaller species (ca. 25 g)  $DEE_{par}$  about equals  $DME_{max}$ , while in the larger species (ca. 10 kg)  $DEE_{par}$  represents only about 60 % of the predicted  $DME_{max}$ . This suggests that limitations in parental effort are more frequently set by the maximum sustainable energy intake in the smaller species than in larger species. Our allometric equation for  $DEE_{par}$  suggests that the relation between BMR, estimated using the equations of Aschoff and Pohl (1970), and the observed parental energy expenditure, is such that on average bird parents work at a daily level somewhere between 3 and 4 times BMR.

## Introduction

The number of offspring an individual produces per attempt is one of the major determinants of its total lifetime reproductive success. Exploration of the limiting factors for brood size in altricial birds is important for understanding differences in reproductive behaviour between species and between individuals within species.

Two different penalties from raising large broods have been identified. Firstly, nestlings in larger broods may suffer from reduced chances of survival both in the nest and after fledging (Lack, 1954). Secondly, increased parental work for the young may entail extra risks for the parents, and thereby threaten their prospects of future reproduction (Royama, 1966; Charnov and Krebs, 1974; Askenmo, 1979). Thus, Drent and Daan (1980) have postulated that optimal parental care for nestlings is associated with a level of daily energy expenditure that represents the maximum that can be sustained without deterioration of the parents' condition. They further suggested that this “optimal working capacity” (Royama, 1966) involves a daily energy expenditure (DEE) for the parents bearing a constant relationship to a species' basal metabolic rate (BMR). This maximal expenditure of

about 4 times BMR is somewhat less than estimates of maximal sustainable energy consumption of 4 to 5 times BMR (Kirkwood, 1983; Daan et al., 1989).

The data presented by Drent and Daan (1980) in support of their proposition were derived from only five species, involving a mixture of studies in captivity and in the field, and of both experimentally enlarged and unmanipulated brood sizes. While the expression of parental effort in terms of DEE was an important step towards specification of strategies of reproductive effort beyond more traditional assays of feeding rates (e.g., Hails and Bryant, 1979; Cronmiller and Thompson, 1980; Tinbergen, 1981; Westerterp et al., 1982), the question of whether or not parental energy expenditure is indeed submaximal still invites further experimentation.

Furthermore, submaximum parental work should give rise to the question of whether optimal work levels are equal for parents raising different numbers of nestlings. Unequal work levels might be expected on theoretical grounds from the trade-off between investment in current and future offspring (Trivers 1972). On the other hand, mechanisms adjusting brood size to food and work conditions might lead to similar work levels in parents of different sized broods.

Our ongoing study on the seasonal cycle of behavioural energetics and proximate and ultimate control of reproductive behaviour in the kestrel (*Falco tinnunculus*; Rijnsdorp et al. 1981; Daan and Aschoff, 1982; Dijkstra et al., 1982; Masman et al., 1986, 1988a, 1988b; Masman and Klaassen, 1987; Daan et al., 1988; Meijer, 1988; Dijkstra et al., 1988a, 1988b; Beukeboom et al., 1988) allows us to evaluate the consequences of variation in brood size for the parents. We discuss here the limiting factors for the rate of food provisioning by the parents. During nestling care the time required for foraging is not a limiting factor since kestrels do not forage for more than 3.0 hours per day even though the daylight lasts ca. 17 hours (Masman et al., 1988b). Even when taking into account the variation in climatic conditions (Masman et al., 1988b) and vole availability (Rijnsdorp et al., 1981) it is obvious that not all profitable foraging time is used by kestrel parents. We have thus evaluated the possibility of energetic constraints by studying the response to manipulations of nestling food demand.

In the kestrel, as in many raptors, the male is exclusively responsible for providing food to the female and nestlings from about two weeks before the first egg is laid until about two weeks after the eggs hatch. During the second two weeks of the nestling phase the female cooperates with the male in providing food to the young, but the male is still responsible for most of the food for the nestlings. Therefore our analysis of parental performance is concerned primarily with male kestrels feeding their broods.

## Methods

### 1. Brood size

In our study area, "Lauwersmeer" (53°20'N, 6°21'E) in the Netherlands, kestrels breed mainly in nestboxes. During the reproductive season (March-August) we

checked about 40 nestboxes weekly to determine laying date, clutch size, brood size and number of fledged young, for each kestrel pair. Clutch size declined from 5.98 eggs ( $n = 50$ ) in the beginning of the season (first half of April) to 3.76 ( $n = 21$ ) in the end of the season (first half of June) and averaged 5.27 ( $n = 492$ ; Dijkstra et al., 1982; Beukeboom et al., 1988). A complete brood contains the same number of chicks as eggs were laid, in an incomplete brood eggs or chicks died.

## 2. Behavioural observations

Between 1977 and 1986 we made behavioural observations of male kestrels tending complete broods. The study area is flat and open, and individual kestrels could be observed virtually continuously from dawn to dusk. For the analyses presented here we selected 32 complete observation days (11 individual males raising 4–7 chicks) on the basis of two criteria: 1) budget time (from beginning to end of observation) exceeded 75 % of the birds' "active day" (i.e. time from dawn civil twilight to dusk civil twilight minus 0.71 h); 2) birds were in sight for more than 75 % of the budget time (Masman et al., 1988b). In the behavioural protocol we distinguished eight different states: directional flight, soaring, flight-hunting (wind hovering bouts alternating with short flight bouts), sitting perched, on the ground, sheltered or in a nestbox. We treated each observation day as an independent data point for male behaviour as related to brood size.

The yield during flight-hunting, the main foraging technique in summer (Masman et al., 1988b), was calculated as the number of prey caught per hour flight-hunting. Daily food intake was also derived from the behavioural protocol and was based on an empirical relationship between prey mass and eating time (see Masman et al., 1986).

## 3. Daily energy expenditure

We calculated daily energy expenditure (Et) using our Time Energy Budget (TEB) model, which was previously validated by use of the Doubly Labeled Water (DLW) method (Masman et al., 1988a). The reconstruction of Et:

$$Et = B + T + A + H + S \text{ kJ} \cdot \text{day}^{-1}$$

was achieved by calculating the basal component (B), a mass specific and circadian phase specific value for energy expenditure under fasting thermoneutral conditions, measured in the laboratory. We augmented this basal level by addition of values for thermoregulation (T), activity (A), heat increment of feeding (H) and for the synthesis of tissues (S), based on local meteorological conditions, behaviour, food intake and individual condition respectively (see for details Masman et al., 1988a).

#### 4. Food requirements of nestlings

In addition to direct measurement of nestling food intake in the field, seven nestlings were handraised in the laboratory under ad libitum food conditions. Four kestrel chicks were taken from a captive brood (Meijer, 1988), at an age of six days, and three chicks were taken from a wild brood at an age of seven days. Chicks were free to move and were held at a temperature of ca. 20° C. Food consisted of freezer-stored common voles (*Microtus arvalis*) trapped in the study area, thawed one day before, and given four times a day at four-hour intervals between 08.00 and 20.00. Food was given until the chicks ignored the food and intake was recorded by weight to the nearest 0.5 g. Total daily food intake per chick was recorded and is presented as the average for the seven chicks.

#### 5. Experiments

To be able to manipulate food availability in the nest we mounted nestboxes against movable sheds, made an opening in the back and posted an observer behind the nestbox in the shed. The whole operation of changing the position of the nestbox and opening the back was carried out step-wise over a period of several days during incubation or young nestling phase. The parents easily adapted to the new situation.

In all experiments we manipulated the energy demand in the nest without changing the brood size as experienced by the parents. The experiments differed in duration and type of manipulation:

I) Surplus food. Between 31 May and 17 June 1980, we carried out three feeding experiments in one nest. We recorded total prey delivery, body mass of nestlings and female, and food intake of the nestlings on control and experimental days. Female body mass and prey mass were determined using an electronic balance. We decreased the food demand by giving extra food (freshly killed laboratory mice) to the nestlings, such that food was available in the nest continuously. The extra food was easily accepted and was fed by the female to the nestlings (< 10 days of age) or immediately eaten by the older nestlings (10–30 days).

II) Food deprivation for 1–3 days. Between 1981 and 1985 12 food deprivation experiments were carried out with broods of different age (Table 1). We recorded parental behaviour, total food delivered to the nest, and body mass change of the nestlings. In broods younger than 10 days we increased the energy demand of the brood by rotating extra nestlings through the nest, of the same age but taken from other nests. Each time the parents delivered a prey and the nestlings had been fed, one or two nestlings were replaced by a hungry nestling. In this way the parents fed four more nestlings than their own brood size. In nests where the nestlings were old enough to take the food themselves (> 10 days) we took away all prey as soon as it was delivered by one of the parents. In this way food intake of the nestlings was virtually zero during the day, and begging behaviour of the nestlings increased notably. In the evening, when the parents had ceased hunting, the nestlings were fed by the observers.

**Table 1.** Food deprivation experiments in kestrel broods. Notes: 1) increase of brood energy demand by rotation of nestlings (see text); 2) deprivation by taking away the delivered food (see text); 3) female disappeared in early nestling phase, before the experiments.

| Year | Male # | Female #          | Clutch size | Brood size | Hatching date | Period of food deprivation                             |
|------|--------|-------------------|-------------|------------|---------------|--|
| 1981 | 397    | 366               | 5           | 5          | May 28        | June 4–5 <sup>1)</sup> , June 25 <sup>2)</sup>         |
| 1981 | 351    | 368               | 6           | 6          | May 23        | June 17 <sup>2)</sup>                                  |
| 1982 | 111    | 109               | 4           | 4          | June 11       | June 23–25 <sup>1)</sup> , June 7–9 <sup>2)</sup>      |
| 1982 | 454    | 450 <sup>3)</sup> | 4           | 4          | June 26       | July 13 <sup>1)</sup> , July 21–22 <sup>2)</sup>       |
| 1983 | 562    | 577               | 7           | 7          | May 20        | May 31–June 1 <sup>1)</sup> , June 15–16 <sup>2)</sup> |
| 1983 | 581    | 596               | 5           | 4          | June 26       | July 14–15 <sup>2)</sup>                               |
| 1985 | 342    | 770               | 6           | 5          | June 13       | July 2–12 <sup>2)</sup>                                |
| 1985 | 775    | 777               | 4           | 4          | June 22       | July 16–22 <sup>2)</sup>                               |

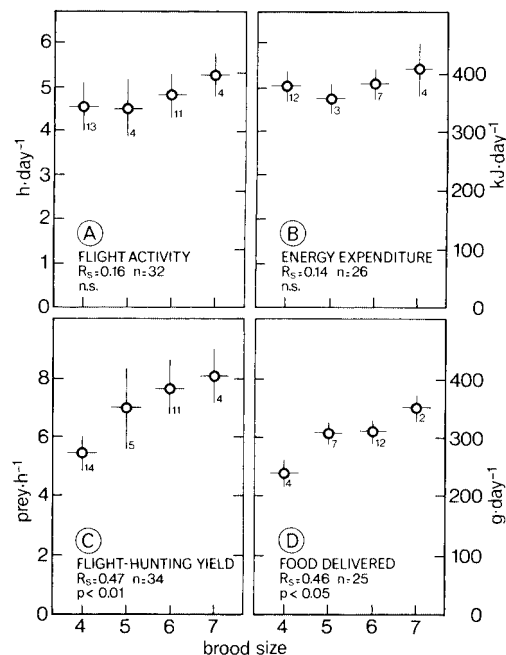
III) Case study with prolonged food deprivation. Between 27 June and 12 July, 1985, one kestrel pair was observed in detail. We deprived the nestlings of food by taking away the food every day for 11 days, starting at a nestling age of 19 days. At the end of each deprivation day the nestlings were again fed by the observers. The parents were observed for complete days every other day. Body mass of the parents was recorded daily with an electronic balance in the nestbox-entrance, connected to a paper chart recorder (Dijkstra et al., 1988a).

Statistical tests were two-tailed throughout unless stated otherwise.

## Results

### 1. Parents raising different numbers of nestlings

During nestling care kestrel males spend on average  $4.75 \text{ h} \cdot \text{d}^{-1}$  (s.d. = 1.55;  $n = 32$ ) in flight activity (Fig. 1A), independent of the number of chicks in the



**Fig. 1.** Performance of male kestrels tending complete (clutch size = brood size), unmanipulated broods of different sizes. A. Flight activity: daily time allocated to directional flight plus flight-hunting; B. Energy expenditure: daily energy expenditure estimated by TEB model, based on complete observation days where activity as well as food intake was recorded completely; C. Flight-hunting yield: mammal prey captured per hour flight-hunting based on days with at least one hour of flight-hunting observed; D. Food delivered: based on observations at close range behind the nestbox. Indicated are means and standard errors; numbers indicate the sample size; correlations were tested with the Spearman Rank-test (one tailed).



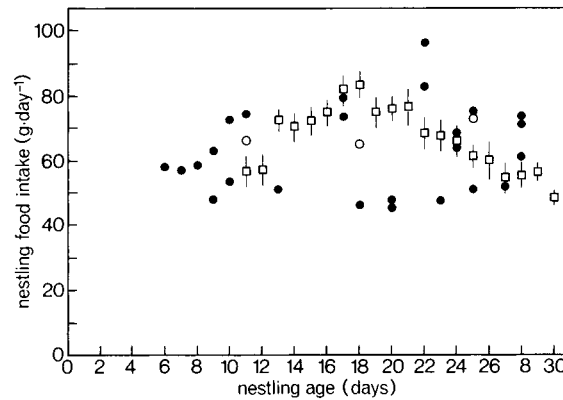
brood (Spearman Rank correlation,  $R_s = 0.16$ ;  $n = 32$ ;  $p > 0.2$ ). Using our TEB model we converted the time budgets into daily energy expenditure ( $E_t$ ), which also showed no correlation between  $E_t$  and brood size ( $R_s = 0.14$ ;  $n = 26$ ;  $p > 0.2$ ). The average  $E_t$  was  $382 \text{ kJ} \cdot \text{d}^{-1}$  (s.d. = 74;  $n = 26$ ; Fig. 1B). Because parental effort was independent of brood size, either the returns during foraging, or the food provisioning rate per chick, must differ between males tending different number of chicks. The flight-hunting yield ( $\text{prey} \cdot \text{h flight-hunting}^{-1}$ ) was positively correlated with brood size (Fig. 1C;  $R_s = 0.47$ ;  $n = 34$ ;  $p < 0.01$ ). By this relationship, a male with seven nestlings was able to obtain 59 % more food with the same daily effort than males with only four nestlings. The number of prey deliveries to the nest per day gives only a rough estimate of food provisioning since prey mass is variable (Masman et al., 1986). Therefore, the amount of food brought to the nestlings was quantified more accurately in a number of cases (25 observation days), where we mounted a nestbox against a shed and observed and weighed the food brought at close range. Total food brought by the male per day increased with brood size (Fig. 1D;  $R_s = 0.46$ ;  $n = 25$ ;  $p < 0.05$ ). The amount of food brought per chick by the male parent decreased slightly with increasing brood size ( $R_s = 0.42$ ;  $n = 25$ ;  $p < 0.05$ ). However, if we consider the total amount of food brought by both parents, including the female's share, this difference disappears ( $R_s = 0.31$ ;  $n = 25$ ;  $p < 0.2$ ) and all broods were provisioned at a rate of  $62.6 \text{ h} \cdot \text{d}^{-1} \cdot \text{chick}^{-1}$  (s.d. = 13.5;  $n = 25$ ).

Daily food intake of kestrel chicks in complete broods in the field varied considerably and was not correlated with nestling age, from 10–30 days of age (Fig. 2, closed symbols). Handraised chicks in the laboratory had an average daily food intake of  $66.8 \text{ g} \cdot \text{day}^{-1}$  (s.d. = 9.9;  $n = 20$ ) which was not significantly different from the average intake in the field ( $62.6 \text{ g} \cdot \text{day}^{-1}$ ; Mann-Whitney U-test;  $p > 0.10$ ). However, food intake in the laboratory showed a trend to increase from day 11 to 18 followed by a decrease over the rest of the nestling period until day 30, a trend not observed in the field (Fig. 2).

## 2. Surplus food

Total prey mass fed by the parents to the nestlings on control days averaged  $63.6 \text{ g} \cdot \text{d}^{-1} \cdot \text{chick}^{-1}$  (s.d. = 14.0;  $n = 5$ ), of which the male provided the major share (93 %). Nestling intake did not vary with age, which is in agreement with the larger data set (Fig. 2). On days when we increased the food satiation of the nest we fed on average 292.3 g freshly killed mice (s.d. = 48.1;  $n = 3$ ) to the brood or  $48.7 \text{ g} \cdot \text{d}^{-1} \cdot \text{chick}^{-1}$ . On these days the male delivered an additional  $19.3 \text{ g} \cdot \text{d}^{-1} \cdot \text{chick}^{-1}$  (s.d. = 6.7;  $n = 3$ ), bringing the total intake to  $68.0 \text{ g} \cdot \text{d}^{-1} \cdot \text{chick}^{-1}$  (open dots in Fig. 2).

The female did not participate in nestling food provisioning under these circumstances, but on the contrary, increased her own daily food intake, which was reflected in her body mass (Fig. 3). Her post-absorptive body mass, recorded at the beginning of the active day, decreased from 260 g on May 31, eight days after egg

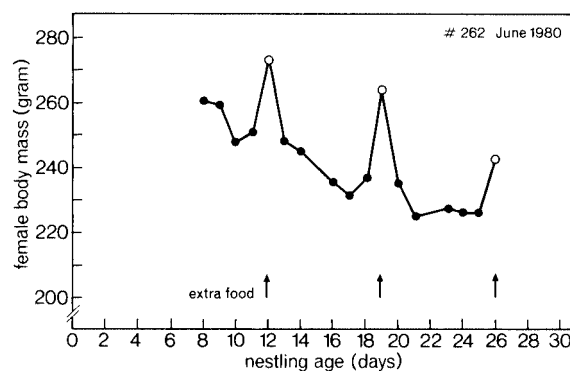


**Fig. 2.** Nestling food intake as a function of nestling age on control days (closed symbols) and days with supplementary food (open dots) in free-living kestrels, and of ad libitum fed nestlings in the laboratory (open squares, indicating daily means  $\pm 1$  SEM for seven handraised chicks).

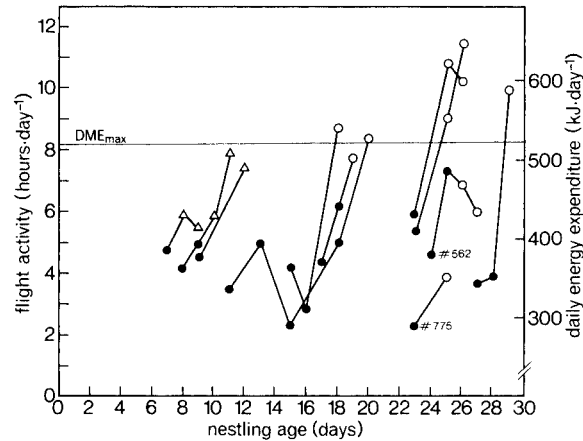
hatching, to 226 g on June 16, with an average decrease on control days of  $-6.8 \text{ g} \cdot \text{d}^{-1}$  (s.d. = 10.4;  $n = 13$ ). The fluctuations of female body mass were strongly affected by the experiments. On days when we gave additional food her mass increased by  $22.0 \text{ g} \cdot \text{d}^{-1}$  (s.d. = 5.0;  $n = 3$ ), and decreased again on the following day (Fig. 3).

### 3. Food deprivation

With broods younger than 10 days, male kestrels spent on average  $4.61 \text{ h} \cdot \text{d}^{-1}$  (s.d. = 0.36;  $n = 4$ ) in flight on control days. Males responded to extra nestlings with



**Fig. 3.** Body mass of female #262 during the nestling phase. Indicated are early morning post-absorptive weights on control days (closed symbols) and on mornings after days with supplementary food (open symbols).



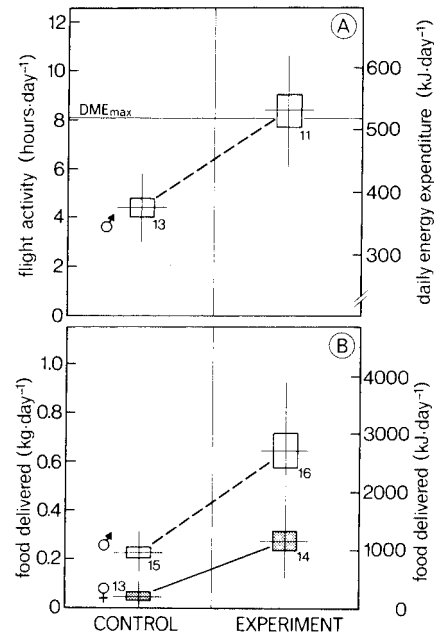
**Fig. 4.** Effect of food deprivation of the nestlings on male activity, total flight per day. Days with food deprivation by rotation of nestlings (see text) indicated by triangles; by taking away the food: open circles; dots indicate control days. Lines connect days of one experiment. Daily energy expenditure (right axis) was estimated from the regression of  $\text{CO}_2$  production (measured by Doubly Labeled Water; Masman and Klaassen, 1987) on flight activity. Horizontal line indicates the estimated daily maximal metabolizable energy intake (Kirkwood, 1983). Two males (#562, #775) showed a deviant response (see text).

an increase (Mann Whitney U-test,  $p < 0.01$ ) to an average of  $6.49 \text{ h} \cdot \text{d}^{-1}$  (s.d. = 1.05;  $n = 5$ ) total flight (open triangles in Fig. 4). With older nestlings ( $> 10$  days) time spent in flight on control days ( $4.46 \text{ h} \cdot \text{d}^{-1}$ ; s.d. = 1.42;  $n = 13$ ) was similar (Mann Whitney U-test,  $p > 0.05$ ) to that in the early nestling phase. However, the response to food deprivation in older nestlings ( $8.41 \text{ h} \cdot \text{d}^{-1}$ ; s.d. = 2.2;  $n = 11$ ; open dots in Fig. 4) was stronger (Mann Whitney U-test,  $p < 0.05$ ).

The average response of male kestrels to experimental food shortage in the nest during the older nestling phase ( $> 10\text{d}$ ) was estimated on the basis of kestrel flight costs (Masman and Klaassen 1987) to be an increase in energy expenditure from  $376 \text{ kJ} \cdot \text{day}^{-1}$  to  $541 \text{ kJ} \cdot \text{day}^{-1}$  (Fig. 5A). Total food brought to the nest increased in correspondence to the increased activity (Fig. 5B). The total amount of food brought during food deprivation by the male ( $646.4 \text{ g} \cdot \text{d}^{-1}$ ; s.d. = 276.7;  $n = 16$ ) which is additional to his own requirements (see Results 4) corresponds with  $2728 \text{ kJ} \cdot \text{d}^{-1}$  metabolizable energy for an adult (Masman et al., 1986). This would be sufficient to cover the demand of about ten nestlings under normal conditions (see above), or the flight activity (costs =  $61.9 \text{ kJ} \cdot \text{h}^{-1}$ ; Masman and Klaassen, 1987) by an adult for more than the available daylight. Thus flight activity in response to nestling food deprivation is not directly limited by available time or energy.

#### 4. Case-study of prolonged food deprivation

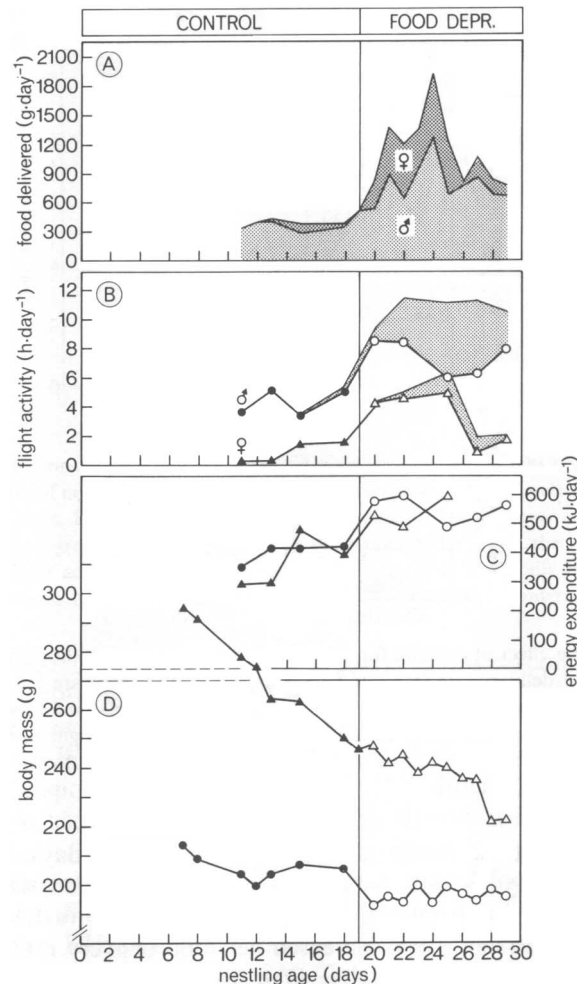
To see whether increased effort could be sustained, we studied the response of one kestrel pair to continuous food deprivation (removal of food by experimenters upon



**Fig. 5.** Summary of the effect of nestling food deprivation in the older nestling phase on flight activity in males (A) and food delivery rate in males and females (B). Indicated are the averages (horizontal lines), s.e.m. (boxes) and s.d. (vertical lines) for control days (left panels) and experimental days (right panels). Numbers indicate sample size in days. Daily energy expenditure (right axes) and  $DME_{max}$  were estimated as in Fig. 4. The energetic equivalent of food deliveries was estimated as metabolizable energy for adults using conversion factors from Masman et al. (1986).

delivery by parents) of the nestlings for eleven consecutive days. The male significantly (Mann Whitney U-test,  $p < 0.001$ ) increased his food delivery rate from  $347 \text{ g} \cdot \text{d}^{-1}$  (s.d. = 54;  $n = 4$ ) on control days to  $788 \text{ g} \cdot \text{d}^{-1}$  (s.d. = 207;  $n = 10$ ) on deprivation days. The female also increased her food delivery rate (Mann Whitney U-test,  $p < 0.01$ ) from  $31 \text{ g} \cdot \text{d}^{-1}$  (s.d. = 43;  $n = 4$ ) to  $354 \text{ g} \cdot \text{d}^{-1}$  (s.d. = 212;  $n = 10$ ; Fig. 6A). This response was essentially equal to that observed in the other experiments (Fig. 5).

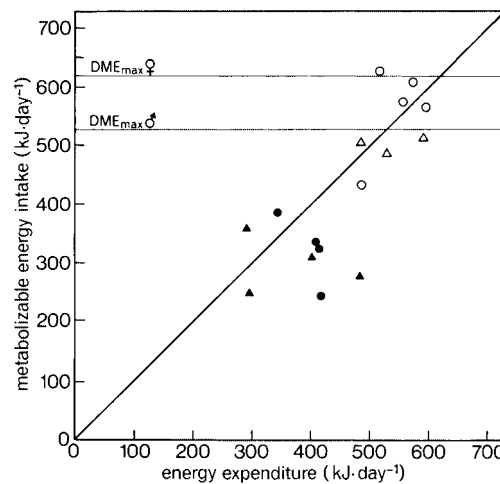
Both parents increased their daily flight activity (Fig. 6B). This increase was partly due to a special situation. The territory of this pair included a dike causing updrafts in which the kestrels could flight-hunt by “hanging” motionlessly, a common behaviour in kestrels in a more hilly environment (Village 1983). The returns during “hanging” were relatively low. During flight-hunting on food deprivation days the yield averaged  $6.78 \text{ voles} \cdot \text{h}^{-1}$  (s.d. = 1.30;  $n = 5$ ) in the male and  $6.35 \text{ voles} \cdot \text{h}^{-1}$  (s.d. = 0.08;  $n = 4$ ) in the female, while the yield during “hanging” averaged  $3.98 \text{ voles} \cdot \text{h}^{-1}$  (s.d. = 0.78;  $n = 4$ ) and  $3.80$  (s.d. = 0.32;  $n = 2$ ) in male and female respectively. We assume that the energetic costs of “hanging” were also very low, and similar to that during soaring (10 % of flight costs; Masman et al., 1988a). The use of this low-cost low-profit hunting technique during



**Fig. 6.** Case study (Box 28, 1985) of the effect of long term food deprivation of a brood (5 nestlings) on: A. Total food delivered per day; B. Flight activity (male: circles, female: triangles on control days (closed) and food deprived days (open), supplemented with the time spent "hanging" (see text), indicated by shading; C. Daily energy expenditure, estimated as in Fig. 1; D. Parental body mass.

increased food demand may indicate a general energy conserving policy of the parents. Nevertheless, in both parents daily energy expenditure increased (Mann Whitney U-test, for male  $p < 0.01$ , female  $p < 0.05$ ) during food deprivation (Fig. 6C).

Body mass of the female decreased during nestling care (Fig. 6D), following the general pattern in female kestrels in our population (Dijkstra et al., 1988a). Daily body mass decrease was not greater during food deprivation than on control days. (Mann Whitney U-test,  $p > 0.05$ ). The male, however, only lost mass at the



**Fig. 7.** Daily energy balance in the male (circles) and female (triangles) of the case study presented in Fig. 6, on control days (closed) and experimental days (open). Line indicates equality of DME and DEE estimated as in Fig. 1. Horizontal lines indicate the estimated  $DME_{max}$  for male (lower) and female (upper) derived from Kirkwood's (1983) equation.

beginning of the experiment, but stabilized in mass during the food deprivation period at an average of 196.4 g (s.d. = 2.8;  $n = 10$ ; Fig. 6D). This indicates that the energy expenditure and metabolizable energy intake of the male were, on average, in balance during the period of increased activity.

Both the male and female increased their energy intake with increased energy expenditure, in response to our manipulation (Fig. 7). Thus this male spent on average 38 % more energy during the food deprivation experiment, delivered 2.3 times more food to the nest, and, nevertheless retained energy balance for these ten days. For this male of 196.4 g (average during food deprivation) Kirkwood's (1983) allometric equation for homeotherms would predict a maximum rate of metabolizable energy intake ( $DME_{max} = 1713 \text{ kg}^{0.72} \text{ kJ} \cdot \text{d}^{-1}$ ) of  $531 \text{ kJ} \cdot \text{d}^{-1}$ . This level indicated in Fig. 7 is slightly less than the observed daily metabolizable energy intake during our experiment, suggesting that the male was performing close to an energetically sustainable maximum.

## Discussion

### 1. Parental effort in different natural brood sizes

Male parental effort of kestrels appeared to be independent of brood size in complete broods, where brood size equalled original clutch size. Food provisioning by both parents was sufficient, so that daily food intake per chick was also independent of brood size, and was moreover on average similar to that of chicks

fed *ad libitum* in the laboratory. However, nestling mortality due to starvation occurs regularly in kestrels, indicating that food provisioning is not always adequate (Daan et al., 1988b). In this study we observed large daily variations in nestling food provisioning in the field. During the early and late nestling phase chicks in the field tended to have a somewhat higher intake than in the laboratory, suggesting that on some days parents may compensate for food shortage caused by unfavourable weather or by a naturally high food demand. The temporary accumulation of reserves by the female during high food availability, as observed during our surplus food experiment, appears to be a functional response in this respect. The extra energy store will make it easier for her to refrain from food intake during periods of poor conditions. We emphasize that by analysing parental performance in complete broods, we probably biased our sample towards parents of good quality in terms of hunting skills and habitat choice. Furthermore we compared parental food provisioning rate with food intake of laboratory raised nestlings, which will have had relatively low requirements for added heat production and activity, and also tended to have slightly higher masses at fledging (30 days of age).

We conclude that clutch size in different kestrels seems to be adjusted to the daily amount of food the males are able to provide to their brood with the same effort. In this way the daily food intake per chick is sufficient and similar in different sized broods. The total amount of food delivered to the nest seems to be set by the males' hunting yield, at a more or less constant level of male daily energy expenditure. The hunting yield, which was shown to be positively correlated with brood size, does not vary with different experimental levels of brood demand (Masman et al., 1988b). Thus hunting yield seems to be set by either the quality of the male or of the territory, or by both. This raises further questions concerning the proximate regulation of clutch size in the kestrel, that are discussed elsewhere (Meijer, 1988; Beukeboom et al., 1988).

## *2. Energetic limitation of kestrel parental effort*

Our food deprivation experiments revealed that male kestrels strongly respond to food shortage in the nest, especially in the older nestling phase (10–30 d). On average they increased daily rate of food delivery to the nest by almost three times, compared to control days, by increasing their activity level. Thereby daily energy expenditure increased considerably and was sustained, in one case up to eleven days, by increasing the metabolizable energy intake correspondingly. Even under considerable food stress about half of the available daylight was left unused for foraging, while the chicks were not satiated, due to continuous removal by experimenters of food delivered by the parents.

Two male parents during the older nestling phase responded differently from the others (Fig. 4). In spite of extreme hunger in its brood of seven nestlings, one male (# 562 Fig. 4) spent only slightly more time in total flight than on control days. This male had a body mass of 168 g just before and 164 g after the experiment, which is extremely low (mean for males in older nestling phase;

193 g; s.d. = 11; n = 28; Dijkstra et al., 1988a). We surmise that a lack of body reserves prevented this bird from increasing its parental effort significantly. The second male (# 775, Fig. 4) reached activity levels during nestling food deprivation similar to the normal control level. This male had a very high hunting yield ( $9.47 \text{ prey} \cdot \text{h}^{-1}$ , s.d. = 0.81; n = 3) and his prey delivery rate during nestling food deprivation thereby reached the same level as that of other experimental males.

We conclude 1) that the mean daily energy expenditure taken on by males during nestling care – to which clutch size is apparently adjusted in anticipation – is well below the maximum they are able to sustain for a few days and 2) that the maximum energy expenditure males are willing to sustain under extremely high nestling demand is not set by the available time for foraging or the available energy in the environment. Two questions have to be considered: 1) What limits the effort of the parent during food deprivation of the nestlings? and 2) Why do parents not normally work at the maximum rate they accept during food deprivation experiments, to increase the number of offspring raised?

During our one experiment on long-term (11-d) food deprivation of nestlings the male increased metabolizable energy intake up to the level of the increased energy expenditure and thus retained energy balance. This suggests that a kestrel male can remain in energy balance at levels of expenditure far above the amount he normally expends. On average the birds operate well below their presumed maximum. During food shortage in the brood the male parent increased activity up to this sustainable maximum, suggesting that there are costs, other than energy expenditure, involved in the increase of parental effort, as discussed below.

In addition to direct energetic consequences, parental effort may entail costs in terms of future survival. Local survival in Pied Flycatcher males (*Ficedula hypoleuca*, Askenmo, 1979) and Blue Tit females (*Parus caeruleus*, Nur, 1984) is reduced in parents of experimentally enlarged broods. The probability of having a second clutch in the same season is reduced in Great Tit females (*Parus major*) after experimental brood enlargements (Tinbergen, 1987; Smith et al., 1987). In the kestrel local survival of parents tending experimentally enlarged broods is also reduced compared to control broods, for both males and females (Dijkstra et al., 1988b). Whether energy expenditure during nestling care is directly causally related to survival over the winter remains to be established. Clearly however, raising enlarged broods may reduce future reproductive success, and this may be an explanation for submaximal parental effort and submaximal clutches.

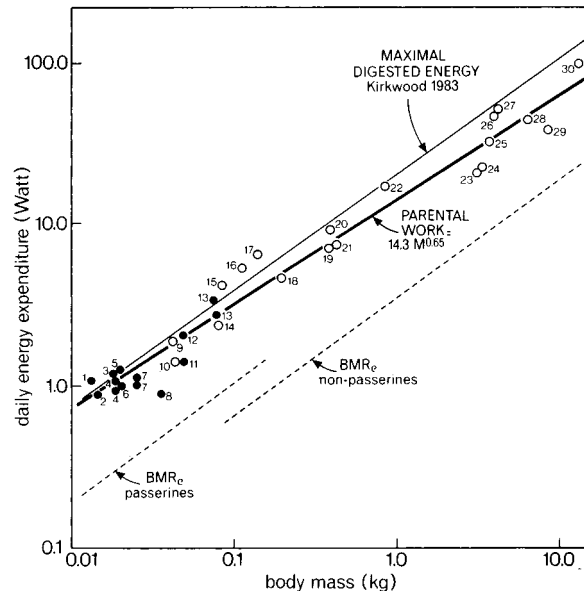
### 3. Interspecific comparison of parental effort

We present here some generalisations about existing energetic limitations during parental care in birds and their relationship to BMR, as postulated by Drent and Daan (1980). The literature provides 32 estimates of daily energy expenditure during parental care in 30 different bird species, all measured with isotopically labelled water. This allows us to derive an allometric relationship for parental effort



**Table 2.** Daily energy expenditure in birds during parental care, measured by labelled water.

| #  | Species                             | Body mass kg | DEE kJ day <sup>-1</sup> | Reference                     |
|----|-------------------------------------|--------------|--------------------------|-------------------------------|
| 1  | <i>Riparia riparia</i>              | 0.0126       | 92.5                     | Turner, 1983                  |
| 2  | <i>Hirundo tahitica</i>             | 0.0141       | 76.6                     | Bryant et al., 1984           |
| 3  | <i>Parus major</i>                  | 0.0177       | 101.1                    | J. M. Tinbergen (unpublished) |
| 4  | <i>Delichon urbica</i>              | 0.0178       | 80.9                     | Hails and Byrant, 1979        |
| 5  |                                     | 0.0182       | 94.5                     | Byrant and Westerterp, 1980   |
| 6  | <i>Hirundo rustica</i>              | 0.0190       | 107.8                    | Turner, 1983                  |
| 7  | <i>Passerculus sandwichensis</i>    | 0.0193       | 86.8                     | Williams, 1987                |
|    | <i>Oenanthe oenanthe</i>            | 0.0243       | 86.8                     | J. Moreno (unpublished)       |
|    |                                     | 0.0243       | 95.3                     | P. Tatner (unpublished)       |
| 8  | <i>Merops viridis</i>               | 0.0338       | 77.4                     | Bryant et al., 1984           |
| 9  | <i>Oceanites oceanites</i>          | 0.0420       | 165.3                    | Obst et al., 1987             |
| 10 | <i>Oceanodroma leucorhoa</i>        | 0.0428       | 122.8                    | Ricklefs et al., 1986         |
| 11 | <i>Mimus polyglottos</i>            | 0.0476       | 121.0                    | Utter, 1971; in Nagy, 1986    |
| 12 | <i>Progne subis</i>                 | 0.0477       | 174.4                    | Utter and Le Febvre, 1973     |
| 13 | <i>Sturnus vulgaris</i>             | 0.0740       | 301.0                    | Ricklefs and Williams, 1984   |
|    |                                     | 0.0775       | 232.9                    | Westerterp and Drent, 1985    |
| 14 | <i>Ceryle rudis</i>                 | 0.0770       | 201.9                    | Reyer and Westerterp, 1985    |
| 15 | <i>Aethia pusilla</i>               | 0.0835       | 357.9                    | Roby and Ricklefs, 1986       |
| 16 | <i>Pelecanoides georgicus</i>       | 0.1092       | 463.5                    | Roby and Ricklefs, 1986       |
| 17 | <i>Pelecanoides urinatrix exsul</i> | 0.1365       | 556.6                    | Roby and Ricklefs, 1986       |
| 18 | <i>Falco tinnunculus</i>            | 0.1923       | 391.5                    | Masman et al., 1988a          |
| 19 | <i>Puffinus pacificus</i>           | 0.3840       | 613.7                    | Ellis, 1984                   |
| 20 | <i>Rissa tridactyla</i>             | 0.3860       | 794.0                    | Gabrielsen et al., 1987       |
| 21 | <i>Cephus grylle</i>                | 0.4200       | 640.2                    | Roby and Ricklefs, 1986       |
| 22 | <i>Uria lomvia</i>                  | 0.8340       | 1475.2                   | Roby and Ricklefs, 1986       |
| 23 | <i>Diomedea immutabilis</i>         | 3.0690       | 1447.0                   | Nagy, 1987                    |
| 24 | <i>Spheniscus demersus</i>          | 3.1700       | 1945.0                   | Nagy et al., 1984             |
| 25 | <i>Eudiptes chrysolophus</i>        | 3.6000       | 2830.4                   | Davids et al., 1983           |
| 26 | <i>Pygoscelis adeliae</i>           | 3.8680       | 4002.0                   | Nagy, 1987                    |
| 27 | <i>Macronectes giganteus</i>        | 4.0440       | 4443.0                   | Nagy, 1987                    |
| 28 | <i>Pygoscelis papua</i>             | 6.2000       | 3803.3                   | Davids et al., 1983           |
| 29 | <i>Diomedea exulans</i>             | 8.4000       | 3320.0                   | Adams et al., 1986            |
| 30 | <i>Aptenodytes patagonica</i>       | 13.0000      | 6851.4                   | Kooyman et al., 1982          |



**Fig. 8.** Daily energy expenditure ( $1 \text{ Watt} = 86.4 \text{ kJ} \cdot \text{d}^{-1}$ ) during parental care in birds, measured by isotopically labelled water. Closed symbols: passerines; open symbols: non-passerines; numbers refer to Table 2. Solid line indicates linear regression of  $\log DEE_{\text{par}}$  on  $\log$  body mass:  $DEE_{\text{par}} = 14.26 \text{ kg}^{0.65} \text{ Watt}$ . Line indicates  $DME_{\text{max}}$  estimated from Kirkwood (1983); dashed lines indicate BMR for passerines and non-passerines in the inactive phase of their daily cycle from Aschoff and Pohl (1970).

(Table 2; Fig. 8), and compare this with maximum daily metabolizable energy intake (Kirkwood, 1983):

$$DME_{\text{max}} = 19.82 \text{ kg}^{0.72} \text{ Watt} \quad (1)$$

The linear regression of log-transformed daily energy expenditure on body mass (kg) for all available studies (Table 2; Fig. 8) yielded the equation for parental daily energy expenditure ( $DEE_{\text{par}}$ ) of:

$$DEE_{\text{par}} = 14.26 \text{ kg}^{0.65} \text{ Watt} \quad (2)$$

$r = 0.983$ ;  $n = 32$ ;  $p < 0.001$ ). The two regressions of  $DME_{\text{max}}$  (eq. 1) and  $DEE_{\text{par}}$  (eq. 2) on body mass have a different slope ( $T = -2.49$ ;  $p < 0.02$ ) such that in a 25 g bird  $DEE_{\text{par}}$  is estimated as 94 % of the predicted  $DME_{\text{max}}$  and in a 10 kg bird  $DEE_{\text{par}}$  is only about 61 % of  $DME_{\text{max}}$ . Thus it seems that the larger species have a parental performance further below their predicted physiological maximum than the smaller species. Several kinds of functional explanations are possible, such as the hypothesis that larger species on average have a longer lifespan and might therefore be more conservative in rate of energy expenditure. Working near the maximal sustainable level might reduce survival and it would be advantageous not to set at

risk the possible occurrences of future reproductive events, which are more likely to occur in larger, longer-lived species than in smaller, shorter-lived species. However, we must recognize that Kirkwood's (1983) equation gives only a crude impression of the actual metabolic capacity of a particular species and is based on both birds and mammals. The actual maxima of DME for the particular bird species in Fig. 8 have not yet been measured.

To be able to express  $DEE_{par}$  in multiples of basal metabolic rate (BMR), using Aschoff and Pohl's (1970) allometric equations for the inactive phase of the daily cycle, we calculated the allometric equations of  $DEE_{par}$  for passerines and non-passerines separately. For passerines (mean mass = 28.6 g; s.d. = 17.8; n = 13; range: 12.6-77.5) the allometric equation for  $DEE_{par}$  is:

$$DEE_{par} = 10.12 \text{ kg}^{0.57} \text{ Watt} \quad (3)$$

( $r = 0.790$ ;  $n = 13$ ;  $p < 0.002$ ). For the average passerine in our sample (28.6 g) this equation estimates a  $DEE_{par}$  of 1.33 Watt ( $115 \text{ kJ} \cdot \text{d}^{-1}$ ), or 3.2 times BMR. For non-passerines (mean mass = 2529.0 g; s.d. = 3507.0; n = 19; range 42-13000 g) parental effort is estimated by:

$$DEE_{par} = 14.73 \text{ kg}^{0.62} \text{ Watt} \quad (4)$$

( $r = 0.975$ ;  $n = 19$ ;  $p < 0.002$ ). For the average non-passerine in our sample (2529 g)  $DEE_{par}$  is estimated as 26.18 Watt ( $2262 \text{ kJ} \cdot \text{d}^{-1}$ ), or 3.7 times BMR.

Our comparison of BMR and  $DEE_{par}$  suggests that parents work at a level somewhere between 3 and 4 times BMR. However, there is a remarkable variation in  $DEE_{par}$  between species of about the same body mass. This has also been recognised for the BMR in species of about the same mass, partly related to latitude (Weathers, 1979) and habitat (Kersten and Piersma, 1987). A more detailed analysis of the relations between BMR and DEE, measured in the same species, and combined with physiological parameters of that same species, is deferred to a future article (S. Daan, L. Groenewold, and D. Masman, in prep.).

It remains uncertain whether parental energy expenditure is optimized at a level associated with BMR, whether it is determined by the maximal sustainable energy intake, or whether all three parameters are interrelated in a predictable way. Further comparative analyses and determination of maximum daily energy assimilation in a number of species are needed to refine the hypotheses. Experimental studies of parental response to the nestling food supply, as presented here for the kestrel, should bring us closer to understanding the nature of parental strategies.

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